Top predators in relation to bathymetry, ice, and krill during austral winter in Marguerite Bay, Antarctica

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ABSTRACT

A key hypothesis guiding the U.S. Southern Ocean Global Ocean Ecosystems Dynamics (U.S. SO GLOBEC) program is that deep across-shelf troughs facilitate the transport of warm and nutrient-rich waters onto the continental shelf of the Western Antarctic Peninsula, resulting in enhanced winter production and prey availability to top predators. We tested aspects of this hypothesis during austral winter by assessing the distribution of the resident pack-ice top predators in relation to these deep across-shelf troughs and by investigating associations between top predators and their prey. Surveys were conducted July-August 2001 and August-September 2002 in Marguerite Bay, Antarctica, with a focus on the main across-shelf trough in the bay, Marguerite Trough. The common pack-ice seabird species were snow petrel (*Pagodroma nivea*, 1.2 individuals km^{-2}), Antarctic petrel (*Thalassoica antarctica*, 0.3 individuals km^{-2}), and Adélie penguin (*Pygoscelis adeliae*, 0.5 individuals km^{-2}). The most common pack-ice pinniped was crabeater seal (*Lobodon carcinophagus*). During both winters, snow and Antarctic petrels were associated with low sea ice concentrations independent of Marguerite Trough, while Adélie penguins occurred in association with this trough. Krill concentrations, both shallow and deep, were also associated with Adélie penguin and snow petrel distributions. During both winters, crabeater seal occurrence was associated with deep krill concentrations and with regions of lower chlorophyll concentration. The area of lower chlorophyll concentrations occurred in an area with complex bathymetry close to land and heavy ice concentrations. Complex or unusual bathymetry via its influence on

physical and biological processes appears to be one of the keys to understanding how top predators survive during the winter in this Antarctic region.

Keywords: Adélie penguin, crabeater seal, krill, habitat associations, bathymetry, Antarctica, Western Antarctic Peninsula, Marguerite Bay

1. Introduction

Physical and biological features operating over different scales have long been known to affect seabird distributions (Hunt and Schneider, 1987), but it is only recently that researchers have begun to understand the mechanisms behind these relationships. For example, in the Arctic, bathymetric features facilitate the formation of fronts that concentrate prey on which seabirds depend during the breeding (Hunt et al., 1998; Russell et al., 1999; Ladd et al., 2005) and nonbreeding seasons (Suryan et al., 2006).

Another physical feature affecting marine top predators in the polar regions is sea ice (Hunt, 1990; Hunt 1991). In Antarctica, sea ice has been shown to be an important determinant of seabird and marine mammal distributions, community structure and composition (Fraser and Ainley, 1986; Ribic et al., 1991; Ainley et al., 1994, 1998; Raymond and Woehler, 2003; Woehler et al., 2003; Chapman et al., 2004; Karnovsky et al., 2006). As a result, Antarctic research is now focusing on how sea ice in combination with other physical factors may attract top predators. One of the leading and oldest hypotheses (Brown, 1980) suggests that this occurs as a result of physical and biological interactions that lead to regions of enhanced productivity.

Testing this hypothesis in the Antarctic has not always produced consistent results, even among seabirds which are the best studied top predators. The response of top predators to enhanced productivity thus still remains poorly understood in the Antarctic (van Franeker, 1992; Veit et al., 1993; Silverman and Veit, 2001; Grunbaum and Veit, 2003). One explanation is that this may be due to the nature of the prey. In the Arctic, studies that focus on fish-eating birds and their prey (e.g., Mehlum et al., 1996; Fauchald et al., 2000) have found stronger correlations than studies in the Antarctic that

focus on seabirds and krill (*Euphasia superba*) (Heinemann et al., 1989; Ryan and Cooper, 1989; Hunt et al., 1992). Hunt (1990) speculated that this mismatch between the results in the Arctic and Antarctic may be due to Antarctic seabirds being less able to locate planktonic prey patches or that Antarctic seabirds are able to fulfill their energy requirements using less dense prey patches.

We suggest an important confounding factor is that most studies addressing this hypothesis have been carried out during the breeding season when resources are assumed to be abundant and seabirds are constrained by the need to return to their breeding colonies. Winter studies may offer a means of disentangling some of these confounding variables because resources are more limited and seabirds are not constrained by having to return to breeding sites. Implied is that, in winter, seabirds are able to associate continuously with their foraging habitat, hence links between their distribution and the biological and physical characteristics of the marine environment should be particularly strong and easier to discern. The linkage of seabird distributions, enhanced production, and physical processes in the Antarctic was first proposed by Fraser and Trivelpiece (1996) based on the summer and winter distributions of Adélie penguins (*Pygoscelis adeliae*).

The multi-disciplinary approach of the U.S. SO GLOBEC program (Hofmann et al., 2002, 2004) provided an opportunity to investigate top predator distributions relative to important biological and physical features of the Western Antarctic Peninsula marine environment during winter. A key hypothesis guiding the SO GLOBEC program is that the action of the Antarctic Circumpolar Current facilitates transport of warm and nutrient-rich Circumpolar Deep Water up onto the continental shelf via deep across-shelf troughs,

resulting in enhanced winter production and prey availability for top predators via sensible heat polynyas (i.e., open water areas resulting from warmer subsurface waters brought to the surface and keeping the surface waters above freezing; Karnovsky et al., 2006). This hypothesis could thus be important to understanding and disentangling how interactions between physical and biological processes affect the winter distribution of Antarctic top predators.

The objective of this paper is to test aspects of the linkage hypothesis by (1) assessing the distribution of the resident pack-ice top predators during austral winter in relation to Marguerite Trough, a major across-shelf trough on the Western Antarctic Peninsula, and (2) investigating associations between top predators and their prey. If deep troughs do facilitate the formation of polynyas and enhanced productivity, we hypothesize that top predators will concentrate in the vicinity of these troughs. We also predict that due to the limited resources available during the winter, top predators will be closely associated with prey patches. This paper builds on Chapman et al. (2004) by focusing on two cruises done during austral winter rather than on cruises during both fall and winter and considering biological variables in addition to physical features.

2. Methods

2.1. Cruise Tracks

Two survey cruises were conducted during austral winter; one during July-August 2001 and the other during August-September 2002. The survey cruises were designed to provide broad-scale studies of Marguerite Bay, with a focus on Marguerite Trough, the main across-shelf trough in the bay; the survey cruises complemented concurrent process-oriented cruises that focused on specific areas of interest in the same study area.

On the survey cruise, seabird and marine mammal observations were made in conjunction with hydrographic, bio-acoustical, primary production, and nutrient surveys on the RVIB *Nathaniel B. Palmer*. The July-August 2001 predator survey was a 28-d effort (99 h during daylight) and covered 828.6 km of trackline (Figure 1a). Air temperature was typically below -10 °C and southwesterly winds periodically reached gale force. Integrated chlorophyll *a* was low (mean = 0.5 mg m^{-2}, S.E. = 0.01). The August-September 2002 predator survey was a 33-d effort (139 h during daylight) and covered 937.4 km of trackline (Figure 1b). Due to heavy ice, the ship was not able to get into Marguerite Bay and only the offshore portion of the grid was surveyed (Figure 1b). Air temperatures during this cruise were typically below 0 ^{o}C, falling below -20 ^{o}C during the period between 21-24 August. Winds were generally toward the east and northeast and periods of strong winds over 30 kts were rare. Integrated chlorophyll *a* in 2002 (mean = 1.2 mg m^{-2}, S.E. = 0.03) was about double that measured in 2001.

2.2 Visual Survey Methods

Predator surveys were conducted while the ship traveled at 4-6 kts, the speed at which a multi-frequency acoustical system was being towed (Lawson et al., 2004). The first and second authors surveyed birds and marine mammals during all daylight hours while the ship was underway. Observers surveyed simultaneously using hand-held binoculars to scan for animals and to confirm species identifications. One observer used 8x and the other used 10x magnification binoculars so that each observer's survey capabilities complemented the other, maximizing the team's ability to detect and identify animals in varied conditions. Observations were made from the bridge (15 m above sea surface) from sunrise to sunset, except when visibility was < 300 m, Beaufort Sea State

was > 5 (following Ainley et al., 1993), or when the ship was stopped at hydrographic stations.

Predator surveys consisted of a continuous 300-m strip transect off the port side of the ship, sweeping from the bow to 90^{o} perpendicular to the ship (Ainley et al., 1994, 1998; the use of a standardized 300-m strip width was proposed by Tasker et al., 1984). Perpendicular distances to seals and penguins on the sea ice were determined using a laser range finder (Leica Geovid 7 X 10 BD Binoculars); distances to flying birds were estimated using a range finder (Heinemann, 1981). A 300-m strip transect width was also used for seal observations (Chapman et al., 2004).

2.3 Data Analysis

2.3.1 Large-scale top predator-environmental variable relationships

To understand the distribution of top predators across the entire study area, statistical models were developed relating the density or presence/absence of top predators to a variety of variables describing the physical and biological environment. The continuous transects were split into 5-km segments. For the July-August 2001 cruise, 135 5-km transects were analyzed; for the August-September 2002 cruise, 153 5-km transects were analyzed. Correlations of bird densities between adjacent transects were low (2001: r = 0.24; 2002: r = -0.12). Potential spatial autocorrelation was also checked for in the analysis (see below).

Seabird densities were calculated using corrections for variation in perceived density resulting from the relative movement of ship and birds (flux, as described in Spear et al., 1992) and with ship-following birds down-weighted (Ainley et al., 1998). Many of the pinnipeds were in the water rather than hauled out onto the ice, which made

density calculations using the NOAA standard protocol problematic (Lakke, 2001). Therefore, presence/absence of pinnipeds was analyzed (Chapman et al., 2004). We calculated the proportion of transects on which each pair of the most common top predators were seen and tested these joint occurrences for significance (Fager, 1957).

Two specific bathymetric features were of interest: Marguerite Trough and the edge of the continental shelf. The 500 m isobath was used to define the location of Marguerite Trough on the continental shelf (see Fig. 1). The 1000 m isobath was used to define the line of separation between the continental shelf and the off-shelf region. We used latitude/longitude and distance to land as general location variables. Calculations of distances and projection of latitude and longitude onto an x-y coordinate system were done using ArcView Geographical Information Systems (Environmental Systems Research Institute Inc. (ESRI), 1996a). Distances to the bathymetric features and to land were calculated using the midpoint of each transect and measuring the shortest distances using ArcView Spatial Analyst (ESRI, 1996b).

Other physical variables used in the models represented bathymetry, water column environment, and sea ice structure (Chapman et al., 2004). Biological variables represented primary and secondary production.

Bathymetric variables were bottom depth and coefficient of variation of bottom depth. Bottom depth for each transect was obtained by interpolating depth values for the midpoint of each transect using high resolution bathymetry data (Bolmer et al., 2004). The coefficient of variation of bottom depth was calculated for each transect by interpolating depth values from the high resolution bathymetry data onto latitude and longitude coordinates generated each minute from the ship's continuous underway

system. Coefficient of variation of bottom depth was used as a measure of bottom topography; more complex bottom topography was represented by higher values of the coefficient of variation.

Due to the amount of sea ice, surface measurements of sea temperature and surface salinity were not available. Therefore, physical water column environment was defined by the temperature maximum below 200 m and salinity at 50 m. These two variables were calculated for each transect using the transect midpoint and interpolating between the closest conductivity-temperature-depth (CTD) stations using ArcView Spatial Analyst (ESRI, 1996b). Each transect was then assigned to a water mass; water mass was defined based on ranges of temperature maximum below 200 m as described in Prézelin et al. (2004). Temperature maximum below 200 m is a reliable index for tracking the intrusions of Circumpolar Deep Water onto the shelf which is hypothesized to enhance primary production and prey availability (Prézelin et al., 2004; Klinck et al., 2004).

Sea ice structure was represented by distance to the sea ice-edge, sea ice type, and sea ice concentration. The sea ice-edge was defined during each cruise through visual analysis of weekly sea ice-concentration analyses of satellite imagery (National Naval Ice Center, Washington, D.C., 2002). The sea ice-edge was defined as the transition region where sea ice covered more than 15% of the ocean surface (Zwally et al., 1983). Distance to the sea ice-edge from each transect midpoint was then calculated using ArcView Spatial Analyst (ESRI, 1996b). During the winter cruises the pack ice had developed well north and west of the study area and all of the survey transects were within the pack ice. The average distance to the sea ice-edge within the ice was 421.3 km

(S.D. = 82.7 km) during the 2001 cruise and 571.3 km (S.D. = 57.6 km) during the 2002 cruise. For analysis, distance to the sea ice-edge was coded to be negative when the ship was in the ice; negative values indicate distance to the ice-edge from within the pack-ice. Sea ice-type was defined using the Antarctic Sea-ice Processes and Climate (ASPeCt) sea ice observation protocol (University of Tasmania, Antarctic CRC, 1998). For analysis, the sea ice types were grouped into the following categories: new ice (grease, nilas, frazil, pancake) and brash, cake ice, floes (small, medium, large), and vast floes. Sea ice concentrations in tenths were averaged across each transect.

We used sea surface chlorophyll *a* integrated to 30 m as an index of primary production. Chlorophyll *a* in the Southern Ocean has been used to index species composition and carbon biomass associated with primary production (Gabriotti et al., 2003, 2005). An association between top predators and chlorophyll *a* could indicate a selection for foraging areas on the scale at which physical or biological processes support higher rates of primary production. For secondary production, Acoustic Doppler Current Profiler (ADCP - 150 Hz) volume backscattering (integrated between 25 and 100 m) was used as an index of zooplankton biomass within the water column potentially available to the top predators. Measures of krill biomass were not available for the entire survey area but were used in a separate analysis (see below).

Chlorophyll *a* concentrations integrated from surface to 30 m depth (mg m^{-2}) from the CTD stations were provided by M. Vernet (Scripps Institute of Oceanography, UCSD, personal communication). These values were then calculated for each transect midpoint by interpolating between the closest CTD stations using ArcView Spatial Analyst (ESRI, 1996b). ADCP volume backscattering (dB) for transects were provided

by M. Zhou and R. Dorland (University of Massachusetts, personal communication); details on their methods can be found in Zhou and Dorland (2004). An integration depth of 100 m was used because 100 m was the average depth at which there was the transition from shallow mixed layer scattering to deeper scattering (Lawson et al., 2004); there were too many missing data to use a deeper integration depth. Due to data quality issues in 2001, ADCP volume backscattering was only used in the analysis of the 2002 data.

Because of nonlinear relationships between species density and the physical variables found by Chapman et al. (2004), we used generalized additive models to model density or presence/absence as a function of the physical and biological variables (Wood, 2006). This approach allows more flexibility in modeling nonlinear relationships, but can also identify linear and polynomial terms where appropriate; we used a gamma of 1.4 to avoid overfitting (Wood, 2006). For flying birds, we modeled birds that were engaged in milling and other non-directional flight behaviors when those behaviors were predominant. Milling and other non-directional flight behaviors are used as indications of feeding. Limiting the data to milling birds was particularly important for snow petrels (*Pagodroma nivea*) in 2002 when ship-followers were a particular problem as the ship broke through the ice. Bird density was log-transformed and modeled with a Gaussian error structure. Presence/absence of pinnipeds was modeled with a binomial error structure.

Models composed of variables corresponding to the physical and biological variables were developed prior to analysis (Burnham and Anderson, 2002). Variables with correlations greater than 0.70 were not used in the same model to avoid potential

problems with multicolinearity (Weisberg, 1985). Akaike's Information Criterion (AIC) corrected for sample size was used to rank the models (Burnham and Anderson, 2002). The model with the minimum AIC value is referred to as the minAIC model. Models within 2 AIC units of the minAIC model are considered competitive models and models within 4 units are considered plausible models (Burnham and Anderson, 2002). Akaike weights (likelihood of model *i*/Σ(likelihoods for all models considered)) were used as a measure of the strength of evidence for the models. The Akaike weights were also used to calculate the relative importance of the variables. Relative variable importance for a variable is the sum of the Akaike weights of models in which the variable is present (Burnham and Anderson, 2002). Deviance explained is reported for all models and adjusted R^2 is reported for models with a Gaussian error structure. All models were checked for autocorrelation in the residuals using spherical semivariograms (Cressie, 1993). Analyses were done in R using *mgcv* (R Development Core Team, 2004). The minAIC models for the species and year combinations are presented in tabular form. We present the relative variable importance values in tabular form; we only report values greater than 0.20 for ease of identifying patterns.

2.3.2 Top predator-prey relationships

To investigate the relationships of top predators and their prey, we looked across the study area (large-scale) and within survey lines using a subset of transects where top predator densities, krill biomass, and an index of zooplankton abundance were concurrently measured. Focal top predators were milling snow petrels, Adélie penguins, and crabeater seals (*Lobodon carcinophagus*). Due to equipment malfunctions (see Lawson et al., *this volume*), we did not have krill biomass estimates for all the transects,

hence investigating top predator-prey relationships was limited to 12 survey lines in 2001 and 15 in 2002 (Fig. 1). Average survey line length in 2001 was 21.1 km (S.E. = 3.4 km) and 27.8 km (S.E. = 3.5). To look at correlations within individual survey lines, we divided individual lines into 500 m segments in order to capture the change in predator densities as a concentration of krill was approached and passed.

Estimates of krill biomass and an index of zooplankton biomass were made from measurements of acoustic volume backscattering (at 120 kHz) collected during acoustic surveys conducted concurrently with visual surveys, using the Bio-Optical Multi-frequency Acoustical and Physical Environmental Recorder (BIOMAPER-II) (Wiebe et al., 2002). During surveys conducted in fall when the region was ice-free, acoustic backscattering arising from krill was identified via a threshold level of -70 dB at 120 kHz derived from krill visual acuity and expected differences in mean volume backscattering between 43 and 120 kHz (Lawson et al., *this volume*). Inversions of mean backscattering at 43, 120, 200, and 420 kHz were then performed to estimate the mean length and density of krill in each acoustically-identified aggregation, and on the basis of these, volumetric biomass was also calculated. During the present winter surveys, however, strong noise associated with ice-breaking led to most of the 43 kHz being unusable. Krill backscattering was therefore identified on the basis of the threshold criterion alone, and wintering biomass estimated on the basis of a target strength derived by assuming a mean length for each aggregation based on the median of all acoustically-estimated lengths from the fall survey for that year. Biomass estimates were vertically integrated in depth ranges of 25-100 m and 101-300 m to yield areal projections of water column krill biomass (kg m^{-2}). Due to bubbles entrained by the passage of the survey vessel, acoustic

estimates of krill and other zooplankton could only be made below a depth of 25 m. We used the same integration depth (i.e., 100 m) as was used for the ADCP data (see above). After correcting for the distance by which the towed body trailed behind the survey vessel, the along-track biomass estimates were then averaged in 500 m segments. The backscattering remaining in the overall acoustic record after krill aggregations were extracted is used here in decibel form (dB) as an index of the biomass of 'other' zooplankton and micronekton, and was similarly integrated in depth and averaged in 500 m segments.

We considered krill and zooplankton/micronekton data separately. We were interested in the more diffuse zooplankton/micronekton in the water column as not all top predators are krill-specialists. Mehlum et al. (1996, 1999) also suggest that it is important to separate biomass due to scattered prey from that of aggregated prey. We used two depth bins, 25-100 m and 101-300 m, as not all top predators are deep divers.

The hypothesis was that top predator densities and prey biomass would be positively correlated both over the survey area and within individual lines. For the analysis over the survey area, we correlated top predator densities and prey biomass using the survey lines, combined over both years, as the sampling units. This gave an indication of large-scale correlations between top predators and prey. Then we focused on within-survey line correlations to understand if top predators were spatially associated with prey at a finer scale. Because the krill biomass, in particular, could extend over consecutive segments, we used wavelet analysis (Torrence and Compo, 1998) to define patches of predators and prey and their linear extent. The linear extent of the patches are a multiple of the number of 0.5 km bins and is considered to be an index of aggregation

size (see Lawson et al., *this volume*, for more refined estimates of krill aggregation size). Within a single survey line, we considered the data to be a combination of signal and error, similar to a time series. Wavelets were used to smooth the data to more clearly delineate the signal (i.e., the patches). In addition, wavelets are flexible enough to model patches which might be single segments along the line. Analyses were done using S+ WAVELETS (Bruce and Gao, 1996). Multiple techniques were evaluated and results were similar; we used the results from nonparametric wavelet shrinkage using default parameters. We also offset the predator distribution by one transect to determine if predators tended to appear before or after a biomass peak along the survey line; this is similar to the cross-correlation analysis of Veit et al. (1993). We restricted the wavelet analyses to survey lines that had large numbers of predators (i.e., predator densities that ranked at the top in the large-scale analysis using the survey lines as the unit of analysis). Using lines with few predators present would not allow us to easily identify predator patches. Lines with few predators may also represent individuals searching for prey (Veit et al., 1993). All correlations were made using Spearman's ρ (Conover, 1999) with an alpha of 0.05 for significance and an alpha of 0.10 for trends.

3. Results

3.1 Winter top predator summary

Over the two years, 5 ice-affiliated bird and 2 pinniped species were seen on the transects. Snow petrel was the most common bird observed (mean = 1.2 birds km $^{-2}$, S.E. = 0.15, n = 288, combined years). Antarctic petrel *(Thalassoica antarctica)* (mean = 0.3 birds km $^{-2}$, S.E. = 0.07) and Adélie penguin (mean = 0.5 birds km $^{-2}$, S.E. = 0.3) were next most common. Crabeater seal was the only commonly seen pinniped; the species

was seen on 23% of the transects (combined years). Species occasionally seen (seen on fewer than 10 transects) in one or both years were Emperor penguin (*Aptenodytes forsteri*), southern giant petrel (*Macronectes giganteus*), southern fulmar (*Fulmarus glacialoides*), kelp gull (*Larus dominicanus*), and Weddell seal (*Leptonychotes wedellii*). The common top predators rarely co-occurred on transects (average proportion = 0.12, n = 12 pairs); the joint occurrences were not significantly different from random ($P > 0.05$, all pairs).

3.2 Top predator-environmental variable relationships

Snow petrel: In 2001, the minAIC model for milling snow petrels consisted of ice concentration, bottom depth, and salinity at 50 m (Table 1). There was a competing model with an almost identical AIC score (within 0.5 AIC units of the minAIC model) composed of ice concentration, bottom depth and chlorophyll (chlorophyll had a negative linear term; Akaike weight = 0.40). Bottom depth and ice concentration were the most important variables as demonstrated by high variable importance weights (Table 2). Salinity at 50 m and chlorophyll were less important (Table 2). In 2002, the minAIC model for milling snow petrels consisted of ice concentration and coefficient of variation of bottom depth (Table 1). The minAIC model had a low Akaike weight (Table 1) but all competitive and plausible models consisted of ice concentration and one other explanatory variable. Ice concentration, therefore, was the most important variable (Table 2). Less important variables were coefficient of variation of bottom depth, temperature maximum below 200 m, and chlorophyll (Table 2).

Milling snow petrels had a nonlinear relationship with ice concentration in both years, with densities being highest in the lighter ice concentrations (Fig. 2a). The two

peaks in the relationship (Fig. 2a) likely reflect sampling bias while the ship traveled through the heavier ice. When in the heavier ice, the ship was forced to travel through leads and other small openings where open water and new ice were also present. Regardless of the nonlinearity, however, milling snow petrels had higher densities in lower ice concentrations. With respect to bathymetry, in 2001, snow petrel densities were lowest in transects over the shallower waters and relatively constant over the deeper waters (Fig. 2b). In 2002, snow petrel densities were higher in areas with less variable bottom topography. In relation to the physical water column environment in 2001, snow petrel densities were highest in transects with an average salinity at 50m of 33.874 psu (S.E. = 0.015, n = 50); these values occurred mainly on transects that were in Upper Circumpolar Deep Water and modified Upper Circumpolar Deep Water.

Antarctic petrel: In 2001, the minAIC model for Antarctic petrels consisted of ice concentration and bottom depth (Table 1). The minAIC model had a low Akaike weight (Table 1) but all competitive and plausible models contained bottom depth. Bottom depth was an important variable followed by ice concentration (Table 2). In 2002, the minAIC model for Antarctic petrel was composed of sea ice concentration, chlorophyll, and distance to land (Table 1). The Akaike weight for the minAIC model was very high, indicating this model was the best of all possible models (Table 1) which was also reflected in the variable importance weights (Table 2).

Like snow petrels, Antarctic petrels were at their highest densities in lighter ice concentrations in both years. The lighter ice concentrations corresponded to areas of brash and new ice. Antarctic petrel densities dropped off quickly as ice concentration increased (Fig. 2c). With respect to bathymetry in 2001, Antarctic petrels were at their

lowest densities in transects over shallower waters; the relationship with depth was similar to that found with snow petrels (e.g., Fig. 2b). With respect to chlorophyll in 2002, Antarctic petrels were at their highest in transects with higher chlorophyll concentrations. A general location variable, distance from land indicated that, in 2002, Antarctic petrel densities were highest in transects between 75 and 125 km from land (Fig. 2d).

Adélie penguin: In 2001, the minAIC model for Adélie penguin consisted of distance to Marguerite Trough, coefficient of variation of bottom depth, and chlorophyll (Table 1). The minAIC model had a low Akaike weight (Table 1) but coefficient of variation of bottom depth was included in all the competitive and plausible models. As a result, in 2001 coefficient of variation of bottom depth was the most important variable followed by bottom depth and distance to Marguerite Trough (Table 2). In 2002, the minAIC model consisted of distance to Marguerite Trough and water mass, though little variance was explained (Table 1). This uncertainty in the best model is reflected in reduced variable importance weights though distance to Marguerite Trough and water mass were the most important variables (Table 2).

Adélie penguins were found near or over Marguerite Trough in both years (Fig. 3a-b). In 2001, the penguins were seen more in the interior of Marguerite Bay over Marguerite Trough (Fig. 3a). In 2001, Adélie penguins occurred over waters with more variable topography (Fig.4a) and in areas of lower chlorophyll. In 2002, transects with higher Adélie penguin densities occurred over Upper Circumpolar Deep Water.

Crabeater seal: In 2001, the minAIC model for the presence of crabeater seals consisted of distance to land and chlorophyll (Table 1). The model closest to the minAIC

model (within 0.45 AIC units of the minAIC model) was the minAIC model with the addition of bottom depth. Chlorophyll and distance to land were the most important variables (Table 2) and appeared in most of the competitive and plausible models. In 2002, the minAIC model consisted of chlorophyll, salinity at 50 m, and distance from Marguerite Trough (Table 1). The Akaike weight for the minAIC model was high, indicating this model was the best of all possible models (Table 1) which was also reflected in the variable importance weights (Table 2).

Although crabeater seals were more likely to occur in areas of lower chlorophyll concentrations in both years, in 2001, some seals occurred in areas of higher chlorophyll concentration as well (Fig. 4b). In 2001, seals were seen closer to land (Fig. 4c) . This reflected two concentrations of seals, one within Marguerite Bay (within an area of higher chlorophyll concentration) and the other off of Alexander Island in the southern part of the study area (Fig. 3c). In 2002, crabeater seals were seen both near to and far from Marguerite Trough resulting in a nonlinear relationship of crabeater seals with distance from Marguerite Trough. Consistent with previous observations in 2001, this nonlinear relationship was due to two concentrations of seals. The first concentration of seals was seen where Marguerite Trough comes close to Adelaide Island and where a polynya had formed; the second concentration of seals was seen off of Alexander Island, far from Marguerite Trough (Fig. 3d). In 2002, crabeater seals also were seen on transects in areas with intermediate values for salinity at 50 m (Fig. 4d); these transects occurred in Modified Upper Circumpolar Deep Water and Upper Circumpolar Deep Water, reflecting the concentrations of seals seen near Adelaide Island and off of Alexander Island, respectively.

3.3 Top predator-prey relationships

Over the study area, both snow petrels and Adélie penguins tended to be positively associated with krill in the 101-300 m depth bin (snow petrel: $\rho = 0.27$, n = 27, $0.05 < P < 0.10$; Adélie penguin $\rho = 0.29$; n = 27, $0.05 < P < 0.10$). Crabeater seals were positively correlated with both krill ($\rho = 0.51$, n = 27, $P < 0.05$) and the zooplankton index in the 101-300m depth bin ($\rho = 0.33$, $P < 0.05$).

Snow petrel: On three lines with the largest numbers of snow petrels, petrels occurred in patches an average of 3.7 km long (S.E. = 0.4 km, n = 7 patches). Along all three lines, snow petrels were associated with zooplankton (either depth bin) or krill (101-300 m bin) (average $\rho = 0.43$; $P < 0.05$ all lines) (Fig. 5, snow petrels were correlated with both zooplankton and krill in the 101-300 m bin; data: $\rho = 0.50$ for zooplankton and 0.39 for krill; $P < 0.05$ both correlations). There were no improvements in the correlations when the data were shifted by one segment.

Adélie penguin: There were six lines where Adélie penguins were seen in groups of 5 or more within the 500 m segments (range = 5 - 22); penguins were not seen in consecutive transects so patch length for the penguins was 0.5 km. On four of the lines, the penguins were positively associated with krill (both depth bins) or zooplankton (101-300 m bin) (average $\rho = 0.35$; $P < 0.05$ all lines). On one line, there were two patches of krill in the 101-300 m bin; the patch with the highest biomass (0.37 kg m^{-2}) occupied only one 0.5 km transect while the patch the penguins were associated with, while not as high in biomass (0.003 kg m^{-2}), was 1.5 km in length (i.e., occupied three consecutive transects). Of interest was one line where Adélie penguins were not associated with their prey; this line started in Marguerite Trough and ended near Adelaide Island. In this case,

the penguins were seen over Marguerite Trough, but the highest prey densities occurred near Adelaide Island away from the Trough (Fig. 5; note peak of penguins before deep krill patches). On only one survey line were correlations improved by shifting the predator densities one segment relative to the prey. On this survey line, the group of penguins was ahead of a peak in zooplankton in the 101-300 m bin by one segment; ρ changed from 0.27 ($P = 0.17$) to 0.45 ($P = 0.03$).

Crabeater seal: There were four lines where crabeater seals occurred in groups of 10 or more within the 500 m segments (range = 10- 20). The seals occurred in patches an average of 2.2 km in length (S.E. = 0.4, n = 6 patches). On three of the 4 lines, krill in the 101-300 m bin formed patches an average of 5.3 km in length (S.E. = 2 km, n = 4 patches) with average biomass of 2.4 kg m^{-2} (S.E. = 1.0) (Figure 5 illustrates the line with the longest patch; average krill biomass in the 101-300 m bin was 2.70 kg m^{-2} with a maximum value of 7.72 kg m^{-2}). Along all three lines, crabeater seals were positively associated with krill in the 101-300 m bin (average $\rho = 0.62$; $P < 0.05$ all lines) (Fig. 5 illustrates the overlap; $\rho = 0.80$ on this line). On the fourth line, where no predator-prey associations were seen, there were two small patches of krill (1 km and 0.5 km in length) though the patches had high biomass (6.14 kg m^{-2} and 5.68 kg m^{-2}, respectively). The largest group of seals occurred 2 km behind the 1 km-length patch. There were no improvements in the correlations when the data were shifted by one segment.

4. Discussion

4.1 Winter community composition

Avian species abundances in Marguerite Bay were low compared to other studies that took place during the Antarctic winter (Ainley et al., 1994; Whitehouse and Veit,

1994). This may be due to the location of the surveys with respect to the ice-edge. The SO GLOBEC surveys were, on average, 400 km or more inside the pack ice, while previous winter studies took place within 150 km of the ice-edge. Adélie penguin densities in Marguerite Bay were over 200 times lower and Antarctic petrel densities were about 4 times lower than those found by Ainley et al. (1994). The only exception was snow petrel, which had comparable densities. Our results demonstrate the near ubiquity of snow petrel throughout the pack ice along the Western Antarctic Peninsula.

Looking at the overlap of seabird communities at the pack ice edge, Ainley et al. (1994) were able to define a winter pack-ice community. However, when we focused only on the pack ice habitat, we did not find species jointly co-occurring on transects. This is similar to the results of Ainley and Boekelheide (1983) who, using data collected in the late spring and early fall, found negative associations of species within the pack ice. They suggested this was due to differential habitat selection, where they defined habitat based on ice characteristics. We also did not observe any feeding flocks during the winter. This was not unexpected since mixed-species groups tend to be seen more frequently along the ice edge or in open water (Fraser et al., 1989; Silverman and Veit, 2001; Chapman et al., 2004).

4.2 Species relationships with physical and biological variables across the study area

Ice characteristics were an important physical feature affecting petrel distributions in the deep pack in our study, consistent with other studies nearer the ice edge (Ainley et al., 1994, 1998). Snow and Antarctic petrels were associated with lighter ice concentrations; these two species use specialized foraging techniques (ambush feeding for snow petrels and pursuit plunging for Antarctic petrels, Ainley et al., 1992) and

access to some open water may be an important factor for these species. In addition, open water may be important if these species use olfactory cues to detect prey as Ainley et al. (1992) speculates for snow petrel and has been found for some open-water Antarctic seabirds (Nevitt, 1999). In 2002, when the association with chlorophyll was positive for both petrels, new and grey ice that occurred in the lighter ice conditions may have been associated with higher chlorophyll values. This would result from higher irradiance available to phytoplankton beneath thinner ice types and that new ice, by definition, covers areas that were recently ice-free. Given the small size of these birds, it is likely they opportunistically exploit less concentrated surface resources not useable by penguins or seals (Fraser et al., 1989) such as individual fish near the water's surface (pers. obs.). A positive relationship with chlorophyll but not zooplankton (ADCP backscattering) for petrels may indicate an association with biological conditions that covary with ice conditions more favorable to foraging by surface-seizing predators.

The inconsistent relationship between petrels and chlorophyll *a* between years may be due to different regional levels of chlorophyll *a* between the years; chlorophyll values in 2002 were twice those seen in 2001. Fauchald and Erikstad (2002) found that the regional abundance of capelin affected their ability to detect correlations between murres and capelin in the Barents Sea during winter, with low prey abundances resulting in poor correlations between predator and prey.

Adélie penguin was the only top predator consistently associated with the deep waters of Marguerite Trough. Surface waters over Marguerite Trough are typically above freezing in winter due to the intrusion of nutrient-rich Circumpolar Deep Water (Klinck et al., 2004). The combination of increased nutrients and increased access to the

water column likely make Marguerite Trough an important area for penguins during the winter (Fraser and Trivelpiece, 1996). Intrusions of Circumpolar Deep Water appear to occur along the Western Antarctic Peninsula (Prézelin et al., 2004) and may help explain the winter movements of and use of areas by Adélie penguins (Fraser and Trivelpiece, 1996; Fraser et al., *this volume*).

Crabeater seals consistently occurred farther from Marguerite Trough in areas where surface chlorophyll was low. These areas were the ice-covered coastal regions near Alexander Island and south, areas found to be important for crabeater seals by Burns et al. (2004) and an area of higher krill concentrations below 100 m (Lawson et al., *this volume*). Burns et al. (2004) argued that crabeater seals used the coastal areas because specific physical features (e.g., complex topography) concentrated prey. If krill do concentrate at deeper depths in the fall and winter along the coastal areas, as indicated by Lawson et al. (*this volume*), only deep diving species would be able to exploit that food resource. Crabeater seals are deep divers and appear to make even deeper dives during the winter, perhaps a change made to follow the change in krill distribution (Burns et al., 2004). A negative relationship between krill and chlorophyll has been found in other studies (Uribe, 1982; Nast and Gieskes, 1986; Loeb et al., 1997), a pattern that has been explained as the product of grazing pressure from krill.

Knowledge of the associations of predators with physical and biological variables in other high latitude systems during the winter is limited. Burger et al. (2004) found a consistent relationship of seabirds with a categorical measure of prey density regardless of season over the continental shelf off Vancouver Island, British Columbia. In contrast, Fauchald et al. (2002) did not find consistent relationships of seabirds with water column

environment (sea surface temperature and salinity) during the winter in the Barents Sea. Much remains to be learned about seabirds and their use of the marine environment during the winter season.

4.3 Top predator-prey relationships

Crabeater seal was the top predator most consistently associated with deep krill patches of enhanced biomass both at the larger spatial scale (across the study area) and at the smaller (within-line) scale. An association with prey density and whales was found by Friedlaender et al. (2006) during the fall in Marguerite Bay. In our study, there were deep krill concentrations smaller than 1 km in length but high in biomass that were not associated with crabeater seals. This may indicate a spatial threshold below which crabeater seals cannot detect krill patches or that predators are more apt to use large patches than small patches of equal quality when resources are sparse (Hunt et al., 1992). Friedlaender et al. (2006) speculated that there was a prey density threshold for whales; specifically that there was a prey density below which it was not energetically efficient for a whale to forage.

Mehlum et al. (1999) found that correlations were stronger between guillemots and aggregated biomass than between guillemots and dispersed biomass. For our top predators, Adélie penguins and snow petrels were associated with krill in the 101-300 m bin at the larger scale but, at the smaller scale, were also associated with prey in the shallower 25-101 m depth bin. The associations with prey in the shallower depth bin likely indicate that these predators are exploiting less concentrated prey higher in the water column that may be associated with general areas of increased prey productivity as reflected in deep krill biomass. Snow petrels feed by surface seizing and Adélie penguins

are able to exploit food on the underside of the ice (Ainley, 2002). However, our ability to measure resources in an important part of the water column for avian predators (i.e., above 25 m) was limited due to bubbles entrained by the passage of the survey vessel.

Seasonality may be a factor affecting the strength of association between predators and their prey. We found strong winter associations between top predators and both aggregated krill and dispersed zooplankton prey. However studies done during the breeding season in the Antarctic have not found correlations to be as strong (e.g., Heinemann et al., 1989; Hunt et al., 1992; Veit et al., 1993). There is a paucity of information in the Arctic outside of the breeding season as well. Suryan et al. (2006) found relationships between short-tailed albatross' (*Phoebastria albatrus*) foraging locations and water column productivity during the non-breeding season (May-November) in the Arctic. But Swartzman and Hunt (2000) found few correlations between seabirds and their prey in the Arctic during the fall when seabirds were migrating. Comparisons between studies are difficult due to characteristics of the system under study (e.g., different prey types utilized by the predators, see Table 8 in Hunt et al., 1992; regional prey differences, Vlietstra, 2005), data collection methods, and different analytical methods. As more data are collected at different seasons, however, what role seasonality plays (if any) will be clarified.

During austral winter, top predators did associate with krill and zooplankton concentrations, consistent with our hypothesis. However, which predators were present and whether they would key in on the resources appeared to depend on the interaction between physical characteristics (e.g., ice concentration, bathymetry) and the characteristics of the prey patches (e.g., patch length, prey biomass). In particular, Adélie

penguins appeared to be associated with Marguerite Trough and stayed there even when there were krill patches of higher biomass near, but outside of, the Trough.

5. Conclusions

Overall, sea ice, bathymetry (including Marguerite Trough), and prey distributions appeared to structure the top predator distributions in Marguerite Bay during austral winter with specific environmental influences depending on the feeding ecology of each species. This is consistent with work on whales in the fall in Marguerite Bay (Thiele et al., 2004; Friedlaender et al., 2006) as well as work done in other systems during other seasons (Hunt et al., 1998; Russell et al., 1999; Yen et al., 2004; Ladd et al., 2005, Suryan et al., 2006). Crabeater seals appeared to be able to track large krill patches, probably a physiological requirement for this species which prepares for breeding during the winter months. On the other hand, petrels appear to depend on ice conditions for access to prey. Given their ability to cover large areas while foraging, they presumably are able to capitalize on more dispersed, less dense prey near the surface. In our study, this prey may consist of zooplankton (including krill) or fish that are more closely associated with the under-ice community. The association of Adélie penguins with Marguerite Trough suggests that this area may have predictable prey, perhaps in lower densities and higher in the water column than patches found in association with seals, as well as reliable access to the water column due to the influence of Circumpolar Deep Water as it moves onto the shelf via the Trough (Klinck et al., 2004). Of the three top predators found in the Antarctic in the winter, the Adélie penguin has the life history traits to take advantage of the foraging opportunities afforded by presence of the Trough.

The combination of bathymetry, ice, and top predator ecology leads to spatial differences in predation pressure on krill. Seals (and to some extent whales, Thiele et al., 2004) were found primarily near Alexander Island and south (also see Burns et al., 2004), where bathymetry is complex close to land, ice concentrations are heavy, and krill were found at deeper depths (Lawson et al., *this volume*). In contrast, seabirds tended to be found near Adelaide Island or in association with Marguerite Trough where productivity is enhanced and ice conditions allowed access to the water column (also see Fraser et al., *this volume*). Though the specific feature of interest of the SO GLOBEC program, Marguerite Trough, was not the only bathymetric feature affecting predator and prey distributions, bathymetry (including the Trough) and its influence on physical and biological processes appear to be key to understanding how top predators with their differing life history strategies survive during austral winter in this Antarctic region.

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Figure Captions

Figure 1. Predator survey locations in the US SO GLOBEC study area during (A) the July-August 2001 cruise and (B) the August-September 2002 cruise. Survey locations are indicated with black lines. The numbered lines are the survey lines where predator and krill data were collected concurrently. The study area is centered on Marguerite Bay (68°29.5' S 70°02.3' W) between Alexander and Adelaide Islands. Marguerite Trough is represented by the 500 m isobath which is indicated by the dotted line. Coastline digital data courtesy of the Antarctic Digital Database Version 3.0, Mapping and Geographic Information Centre, British Antarctic Survey.

Figure 2. Nonlinear relationships for variables from the minimum AIC models of top predator density and physical-biological variables using 5 km survey transects made during the July-August, 2001 cruise (A-C) and the August-September, 2002 cruise (D) in the US SO GLOBEC study area. The relationships are (A) snow petrel density in relation to ice concentration, (B) snow petrel density in relation to bottom depth, (C) Antarctic petrel density in relation to ice concentration, and (D) Antarctic petrel density in relation to distance to land.

Figure 3. Relative density for Adélie penguin (A, B) and crabeater seal (C, D) in relation to Marguerite Trough using 5 km survey transects made during the July-August, 2001 cruise (A, C) and the August-September, 2002 cruise (B, D). Marguerite Trough is represented by the 500 m isobath which is indicated by the dotted line. Densities were standardized with the mean and standard deviation (SD Standardization) so data for both

top predators could be plotted on the same map and areas of concentration could be directly compared. In 2001, mean density was 0.15 individuals km^{-2} for Adélie penguin and 0.16 individuals km^{-2} for crabeater seal. In 2002, mean density was 0.06 individuals km^{-2} for Adélie penguin and 0.11 individuals km^{-2} for crabeater seal. See Figure 1 for data source and map location.

Figure 4. Nonlinear relationships for variables from the minimum AIC models of top predator density/occurrence and physical-biological variables using 5 km survey transects made during the July-August, 2001 cruise (A-C) and the August-September, 2002 cruise (D) in the US SO GLOBEC study area. The relationships are (A) Adélie penguin density in relation to coefficient of variation of bottom depth, (B) crabeater seal occurrence in relation to chlorophyll *a*, (C) crabeater seal occurrence in relation to distance to land, and (D) crabeater seal occurrence in relation to salinity at 50 m.

Figure 5. Distribution of top predator densities (top plot), krill density and zooplankton index (middle plot), and the echogram (lowest plot) for Julian Day 250 in 2002 (line 14 in Fig. 1b). For predator densities (number 500 m^{-1}), solid black line = Adélie penguin, dotted black line = crabeater seal, and solid blue-grey line = snow petrel. For the krill biomass estimates (kg m^{-2}) and zooplankton index (dB), dashed black line = krill in the 25-100 m depth bin, solid black line = krill in the 101-300 m depth bin, dashed blue-grey line = zooplankton index in the 25-100 m depth bin, and solid blue-grey line = zooplankton index in the 101-300 m depth bin. For the echogram, the color scale indicates volume backscattering strength at 120 kHz in decibels. Blue represents low

backscattering while red to black indicates high backscattering. White indicates no data which includes the shallow zigzagging trace representing the path of the BIOMAPER-II, the uppermost portion of the water column where the surface bubble layer has been excised, regions where bottom echoes have been excised, and areas falling beyond the maximum range of the acoustic system (300 m below the towed body). Gaps in the echogram indicate areas where BIOMAPER-II was not in the water. The krill biomass and zooplankton index were only calculated where overlapping predator data were available.

Table 1. The minimum AIC model for each species/year combination for seabirds and pinnipeds seen during winter in Marguerite Bay, Antarctica, 2001-2002. s(variable)=nonlinear relationship fit using a spline smoother. Otherwise, variables in brackets have a negative linear relationship with the response and variables without brackets have a positive linear response. Variables are defined in the Methods.

Species	Year	models	Akaike weight	Deviance explained	adj R^2
milling snow petrel	2001	s(Ice concentration) + s(Bottom depth)+ [Salinity 50 m]	0.52	0.52	0.47
	2002	s(Ice concentration) + [Coefficient of variation (bottom depth)]	0.27	0.27	0.24
Antarctic petrel	2001	s(Ice concentration) + s(Bottom Depth)	0.17	0.32	0.27
	2002	[Ice concentration] + Chlorophyll + s(Distance to land)	0.95	0.55	0.52
Adélie penguin	2001	[Distance from Marguerite Trough] + s(Coefficient of variation(bottom depth)) + [Chlorophyll]	0.25	0.28	0.25
	2002	[Distance from Marguerite Trough] + Water mass	0.43	0.12	0.09
crabeater seal	2001	s(Chlorophyll) +s (Distance to land)	0.31	0.39	
	2002	[Chlorophyll] + s(Salinity 50 m) + s(Distance from Marguerite Trough)	0.96	0.38	

Table 2. Relative variable importance for physical and biological variables considered in modeling the distribution of seabirds and pinnipeds in Marguerite Bay during winter 2001 and 2002. Variables are defined in the Methods. Relative variable importance for a variable is the sum of the Akaike weights of models in which the variable is present. Only variables with a weight of 0.20 or greater are presented.

	Species							
	milling snow petrel		Antarctic petrel		Adélie penguin		crabeater seal	
Variable	2001	2002	2001	2002	2001	2002	2001	2002
Bathymetry								
Bottom depth	0.98		1		0.57		0.44	
Coefficient of variation of bottom depth		0.27			1			
Sea Ice structure								
Distance to ice edge			0.21		0.24	0.36	0.29	
Sea ice type								
Sea ice concentration	1	1	0.31	1				
Water column environment								
Water mass						0.55		
Salinity at 50 m	0.58		0.25					1
Temperature maximum below 200 m		0.23						
Plankton biomass								
Chlorophyll integrated to 30 m	0.41	0.22		1	0.33		0.83	1
ADCP volume backscattering (25-100 m)								
Specific Features								
Marguerite Trough			0.22		0.43	0.52		0.96
Shelf break					0.27			
Location								
Distance to land				1			0.60	
Latitude/longitude								

Fig. 1

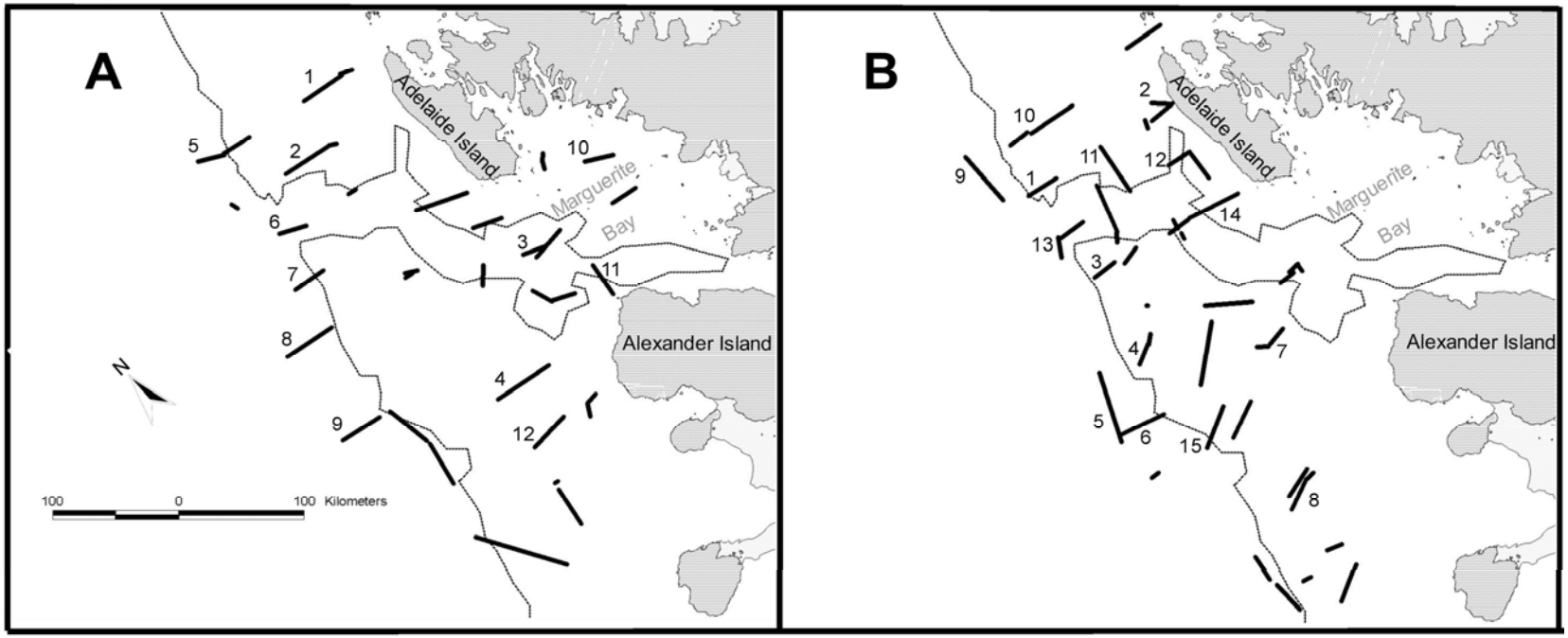

A
Adelaide Island
Marguerite Bay
Alexander Island
N
100 0 100 Kilometers
B
Adelaide Island
Marguerite Bay
Alexander Island

Fig. 2

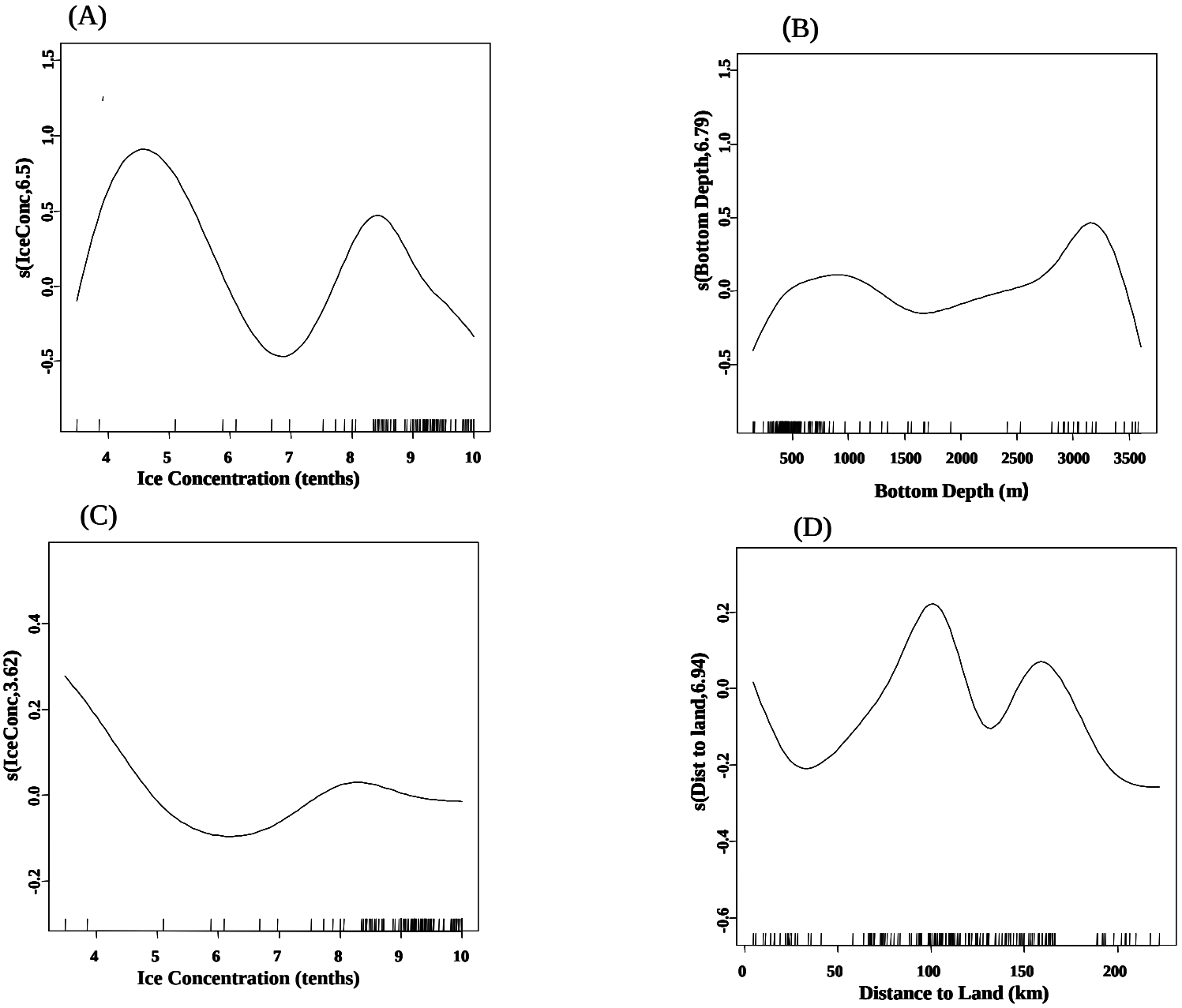

(A)
s(IceConc,6.5)
Ice Concentration (tenths)
(B)
s(Bottom Depth,6.79)
Bottom Depth (m)
(C)
s(IceConc,3.62)
Ice Concentration (tenths)
(D)
s(Dist to land,6.94)
Distance to Land (km)

Fig. 3

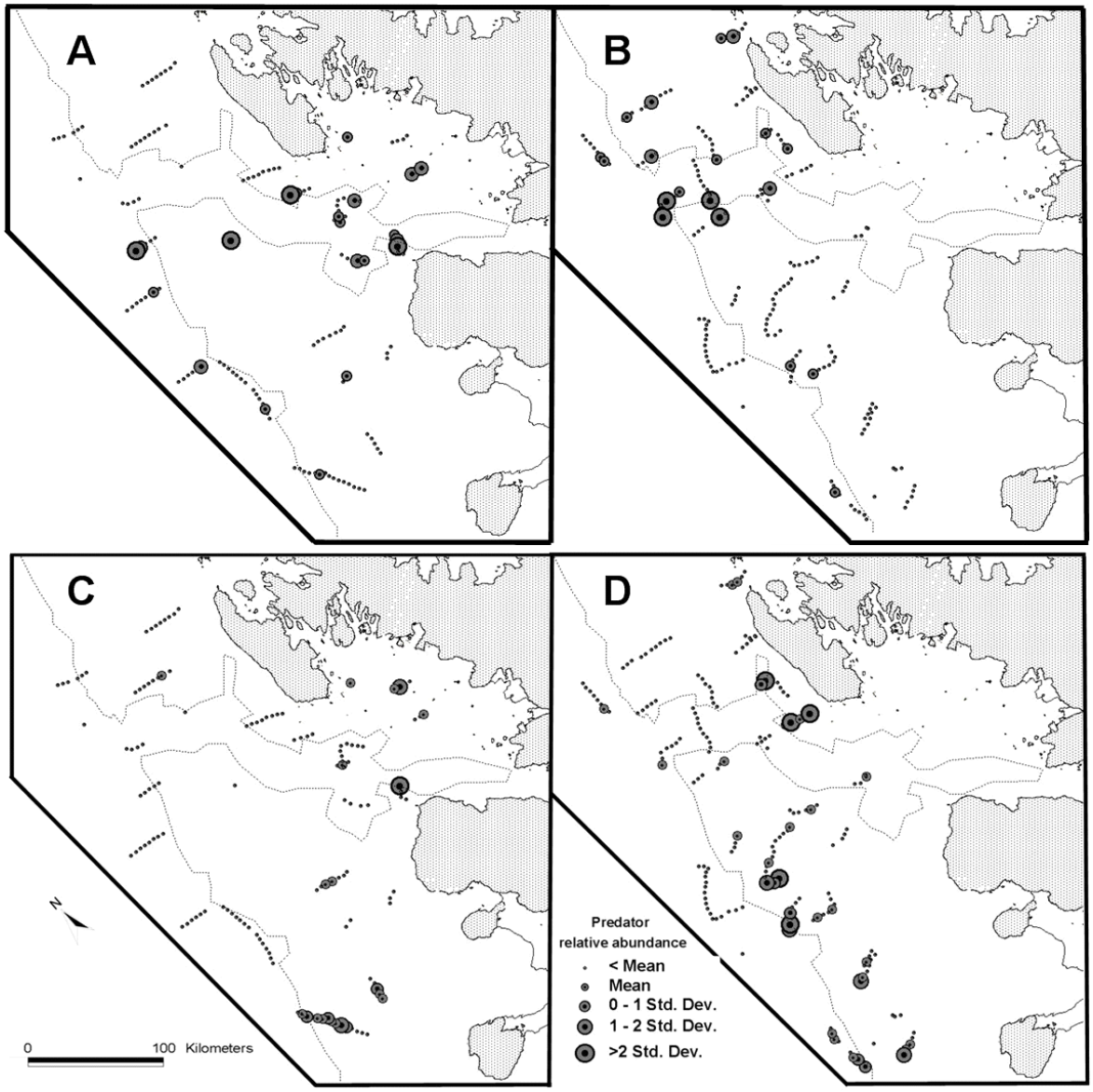

A
B
C
D
N
0
100 Kilometers
Predator
relative abundance
< Mean
Mean
0 - 1 Std. Dev.
1 - 2 Std. Dev.
>2 Std. Dev.

Fig. 4

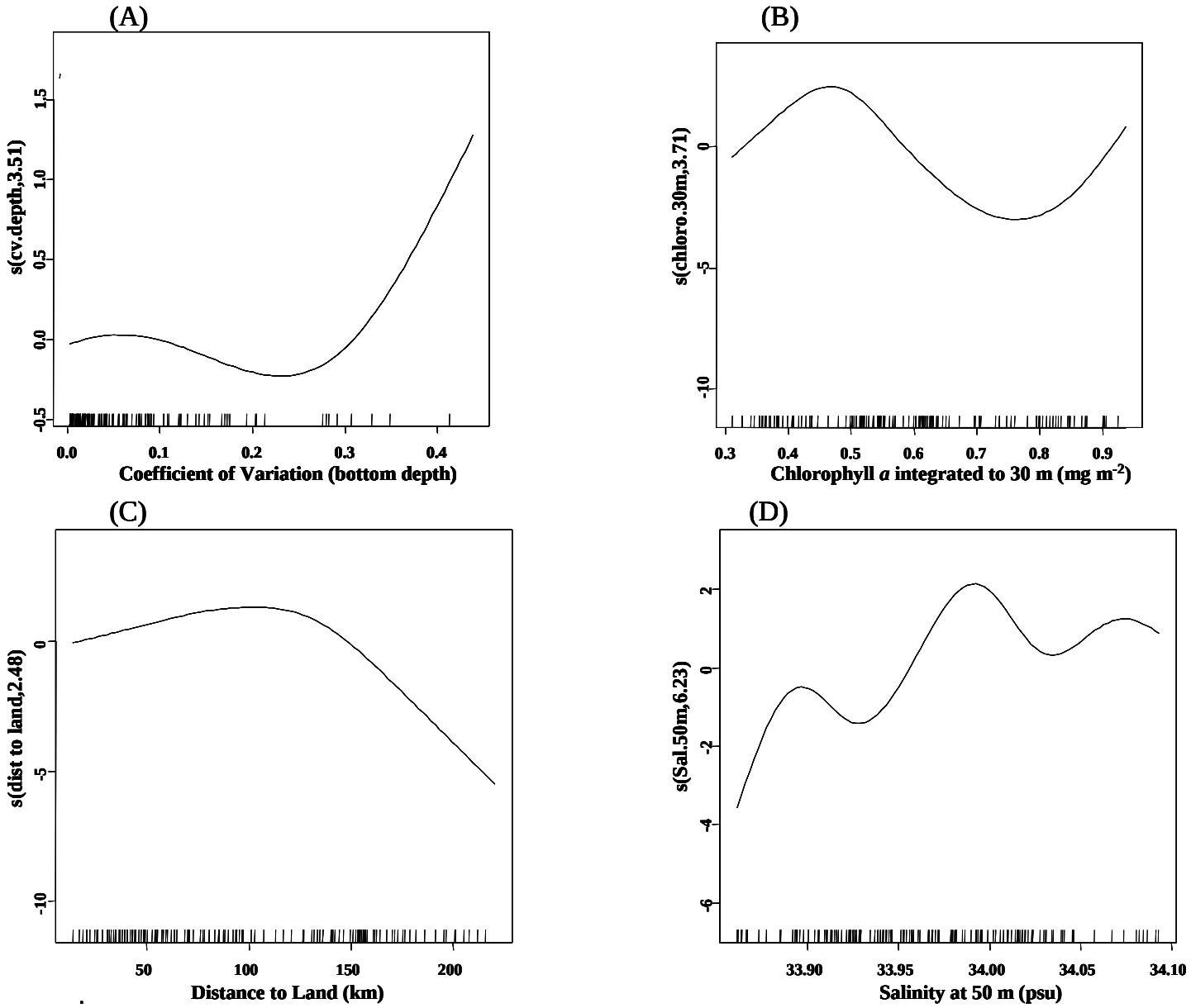
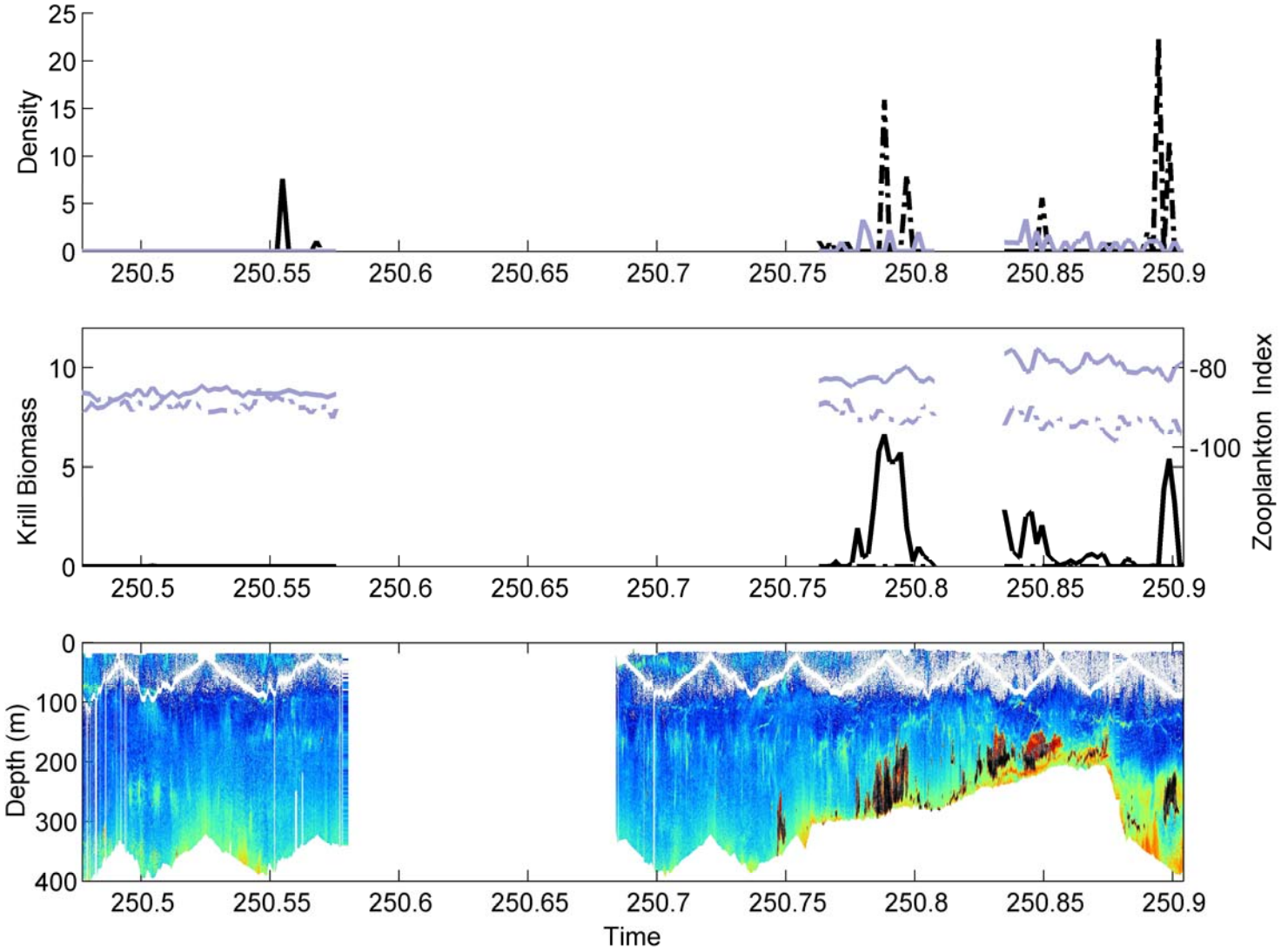

(A)
s(cv.depth,3.51)
-0.5
0.0
0.5
1.0
1.5
0.0
0.1
0.2
0.3
0.4
Coefficient of Variation (bottom depth)
(B)
s(chloro.30m,3.71)
-10
-5
0
0.3
0.4
0.5
0.6
0.7
0.8
0.9
Chlorophyll a integrated to 30 m (mg m-2)
(C)
s(dist to land,2.48)
-10
-5
0
50
100
150
200
Distance to Land (km)
(D)
s(Sal.50m,6.23)
-6
-4
-2
0
2
33.90
33.95
34.00
34.05
34.10
Salinity at 50 m (psu)

Fig. 5


Density
25
20
15
10
5
0
250.5
250.55
250.6
250.65
250.7
250.75
250.8
250.85
250.9
Krill Biomass
10
5
0
-80
-100
Zooplankton Index
Depth (m)
0
100
200
300
400
Time